

1^{ER} PRIX DU CONCOURS DE RÉDACTION SCIENTIFIQUE GEORGES-MAHEUX

BEHAVIOURAL MECHANISMS OF LARVAL SOCIETIES

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Introduction

Eusocial insects, such as ants, termites and bees, represent only one end of the broad spectrum of insect sociality. The larvae of several groups of phytophagous insects – Lepidoptera, Symphyta (Hymenoptera), Chrysomelidae and Curculionidae (Coleoptera) – have also converged on a lifestyle that includes group living. Although there are inherent disadvantages to group living, such as increased competition for resources, increased pathogen transmission and conspicuousness that could attract predators, plant-feeding insects may benefit in various ways from being in a group (Fitzgerald 1993). Proposed selective advantages of larval aggregation include increased feeding efficiency (Clark & Faeth 1997; Denno & Benrey 1997), enhanced group defence against predators (Vulinec 1990), and improved thermoregulation (see Casey 1993 and references therein). However, in order to benefit from advantages accruing through sociality, the members of a colony must maintain group cohesion and coordinate their activities. These insect groups have been shown to exhibit remarkably diverse social complexity, with considerable communication among group members (Costa & Louque 2001; Costa *et al.* 2003; Costa *et al.* 2004; Fitzgerald 1995; Fitzgerald & Underwood 1998a, b; Ruf & Fiedler 2002). Although the adaptive value of collective foraging has long been a subject of interest, the study of its underlying mechanisms is a recent addition. Costa & Fitzgerald (1996) have suggested that non-reproductive systems that exhibit communication and cooperation may prove to be the most useful communities to study in order to understand the determinants of social phenomena. Accordingly, a better documentation of the range and diversity of social forms and means of communication among group-living non-eusocial species should lead to a better understanding of social evolutionary pathways in these groups.

Communication in larval communities

In many social species, contact with group members is maintained via trail pheromones (Costa & Louque 2001; Costa *et al.* 2003; Fitzgerald & Peterson 1988;

Fitzgerald & Underwood 1998b; Ruf *et al.* 2001). Tactile cues constitute another important means of communication, often in combination with trail pheromones. Tactile contact probably promotes grouping or foraging in many social caterpillar and sawfly species (see Costa *et al.* 2003; Flowers & Costa 2003). For example, in the forest tent caterpillar (*Malacosoma disstria*), young caterpillars were shown to exhibit leader following, which was suggested to be particularly important in exploring unmarked territory (Colasurdo & Despland 2005).

Processionary behaviour is a coordinated form of locomotion in which cohorts of insects travel in a single file, in head-to-tail contact. This behaviour is distinct from trail following in that trail followers move independently and typically at a distance from each other, referring themselves to a trail marker to stay in line rather than contact stimuli associated with the bodies of their siblings. Processionary behaviour occurs most commonly in the subfamily Hemileucinae of the Saturniidae, and has been investigated in *Hemileuca* and *Hylesia* (Fitzgerald & Pescador-Rubio 2002; see references in Fitzgerald *et al.* 2004). It is also particularly well developed in the Notodontidae genera *Thaumetopoea* (Fitzgerald 2003) and *Orchrogaster* (see references in Fitzgerald *et al.* 2004). In the processionary caterpillar *Hylesia lineata* and the pine processionary caterpillar (*Thaumetopoea pityocampa*), both thigmotactic and chemical cues have been shown to play a role in maintaining processions (Fitzgerald & Pescador-Rubio 2002; Fitzgerald 2003). Among the beetles, the Neotropical weevil *Phelypera distigma* was shown to travel in processionary columns, and trail pheromones were shown to allow stragglers to catch up with processions that had gotten ahead of them (Costa *et al.* 2004).

Group foraging

Fitzgerald & Peterson (1988) classified social larval communities as patch-restricted, nomadic or central-place foragers (or a combination of these), depending on whether they feed within their home webs, travel between different resource patches, or use a communal nesting site which they leave periodically to forage.



Trail pheromones are central components of the communication systems of these societies and as such their properties can be expected to be fine-tuned to the needs of the colonies. Fade-out time is an important feature of the trail pheromones of Lepidoptera larvae. The trails of the central-place foragers *Malacosoma* (Fitzgerald 1995), *Eucheira* (Fitzgerald & Underwood 1998b), *Gloveria* (Fitzgerald & Underwood 1998a), *Thaumetopoea* (Fitzgerald 2003), and *Eriogaster* (Ruf *et al.* 2001; Ruf & Fiedler 2002) all have long-lived components that facilitate the colony's return to profitable feeding sites for days after their initial discovery. They avoid the confusion that might occur if their foraging arenas became cluttered with long-lived trails by incorporating into the trails a labile component that allows them to ascertain relative trail age. In comparison, the trail pheromone of *P. distigma* is remarkably short-lived (Costa *et al.* 2004). The reason for this difference may be that the weevil larvae are nomadic foragers moving only short distances from one feeding site to the next.

The complexity of information encoded in the trails also varies and has been a central issue in previous studies. In nomadic and patch-restricted foragers, chemical cues often only serve as a cohesive device and contain little or no foraging information and fail to elicit recruitment (Fitzgerald & Costa 1986). This is because caterpillars living near their food (patch-restricted and nomadic foragers) have no need to assist one another in finding food sources. As local patches are exhausted, patch-restricted foragers may simply expand the spatial bounds of their colony to adjacent patches, whereas nomadic foragers typically move to a new patch. In contrast to these foraging modes, central-place foragers may benefit from coordinated orientation towards food patches. Studies have shown that successful foragers of the small eggar moth (*E. lanestris*), the lackey moth (*Malacosoma neustria*) and the eastern tent caterpillar (*M. americanum*) encode foraging information in their pheromone trails and direct unfed group members to the most profitable food sources (Fitzgerald & Peterson 1983; Fitzgerald & Costa 1999; Peterson 1988). Fitzgerald & Underwood (1998b) suggested that the patchiness of the food supply and the need to search extensively for food may have led to the evolution of the fine-tuned foraging system of *M. americanum*. Also, the larval development of *E. lanestris* and *M. americanum* seems to be selected for speed, as these caterpillars hatch in early spring. For more slowly developing caterpillars which forage strictly at night – such as *Gloveria* and *Eucheira* – there are possibly no selective advantages to develop a highly sophisticated foraging system, characterised

by short and efficient foraging bouts, such as those exhibited by *M. americanum* and *E. lanestris* (Fitzgerald & Underwood 1998b).

Synchronised foraging schedules of gregarious species have been postulated to depend either on the avoidance of visual predators or on the effect of temperature on the physiology of ectotherms, and the resulting foraging schedules are therefore highly variable. Some species are diurnal, others are nocturnal, and others forage both day and night (see references in Ruf & Fiedler 2002). The plasticity of foraging schedules with regard to environmental variability also differs between species: the eastern tent caterpillar (*M. americanum*) and the madrone caterpillar (*E. socialis*) both exhibit fixed circadian foraging schedules (Fitzgerald *et al.* 1988; Fitzgerald & Underwood 1998b). In this case,



Malacosoma disstria larvae.

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behaviour is constrained by the occurrence of synchronising cues and does not necessarily reflect or meet individual requirements. For instance, if daybreak rather than hunger level triggers foraging, the timing of foraging will be synchronous among individuals but not necessarily in line with their feeding requirements. In fact, Fitzgerald & Visscher (1996) showed that eastern tent caterpillar colonies forage less frequently than do isolated individuals and postulated that strong selection pressure for synchronous foraging can override the tendency of individuals to forage according to their own hunger levels. They suggested that if foraging by individual caterpillars was mediated by temperature, it might be difficult to keep colony activities synchronous (Casey *et al.* 1988). However, the small egg moth caterpillar (*E. lanestris*) and the forest tent caterpillar (*M. disstris*) can undertake foraging bouts at different times of day and foraging is highly influenced by temperature (Ruf & Fiedler 2002; Peters & Despland 2006). This plasticity can improve group member's ability to meet their requirements in different environments.

However, little is known on how group members reach a consensus on the timing of foraging bouts. Long (1955) demonstrated that in larval groups of the large white butterfly (*Pieris brassicae*) and of the silver-Y moth (*Plusia gamma*), movement of an individual larva together with a sense of its direction was conveyed to adjacent larvae. Rands *et al.* (2003) suggested the spontaneous emergence of temporary "leaders" and "followers" owing to the build-up of differences in energetic state. The individual with the lowest reserves emerges as the "pace-maker" and determines when the pair should forage. Most species that forage in groups do so *en masse*, and this reluctance to forage individually has been suggested to serve in maintaining colony cohesion during exploration of a new territory (Colasurdo & Despland 2005). If the individuals with the lowest reserves determine when the group should forage, one might expect that as the number of hungry individuals increases, so does the level of restlessness within the group. It is likely that an increase in the number of physical contacts between individuals may be an important cue to determine when the group should forage, in which case one might wonder which individuals take the lead.

Follow the leader

Not only is trail lying during exploratory foraging costly, but the leader is more likely to be at risk of succumbing to small predators that lie in wait, such as spiders, since the leader would likely be the first to move within striking distance of the predators and would be

unprotected from frontal attack. In the pine processionary caterpillar (*T. pityocampa*), Fitzgerald (2003) found that leaders of above-ground processions spend more energy in locomotion than other caterpillars in the processions, and thus followers enjoy an economy of movement at the expense of the leader. Fitzgerald (2003) also suggested that judging from their hesitant locomotion, caterpillars in the vanguard might be reluctant leaders, goaded on by the caterpillars that line up behind them. In tent caterpillars, previous studies have shown that individuals in the vanguard only advance a short distance and turn back frequently (Fitzgerald & Costa 1986; Peterson 1988). Although a caterpillar in the vanguard is more likely to turn back, it is usually replaced by another, and as colony mates move onto the newly marked trail, they reinforce it, encouraging the group to advance. This effectively pushes forward the end of the trail, allowing the group to slowly progress (Fitzgerald & Costa 1986).

Interestingly, laboratory studies showed that females of the pine processionary caterpillar (*T. pityocampa*) lead processions more often than males, indicating that the colonies may have a gender-based division of labour (polyethism), with females predisposed to spend more energy and expose themselves to more risks than males (Fitzgerald 2003). In colonies of the madrone caterpillar (*E. socialis*), Underwood & Shapiro (1999) also reported a gender-based division of labour in which the male caterpillars were more likely to spin silk and lay down foraging trails than the females; however, this does not appear to be the norm. Although polyethism was reported in social caterpillars by Wellington (1957), who argued that colonies of tent caterpillars consisted of an adaptive mixture of siblings with different activity levels, subsequent studies (Edgerly & Fitzgerald 1982) have failed to support these earlier studies and cast doubt on the occurrence of polyethism in tent caterpillars. Similarly, Flowers & Costa (2003) found that movement by the red-headed pine sawfly (*N. lecontei*) was not consistently led by any particular subset of larvae.

In most species, the difference in physiological state may be important in determining which individuals are in the vanguard and their likelihood of turning back or establishing trails. Starved individuals might be expected to modify their positions relative to neighbours as a function of their internal state and tend to occupy positions towards the front of the group, being more willing to risk dangerous positions if that will benefit their resource intake (Fitzgerald 2003). However, when the advantage of being in a frontal position is outweighed





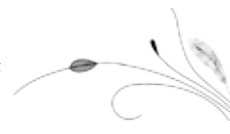
by the perceived risk of predation, one might expect that individuals will avoid the front of the group and perhaps look for positions at the centre of the group. In which case, alternating between the position of leader or follower within the group might be a trade-off between being the first to encounter a food source and the risk of encountering predators.

Research perspectives

Mathematical modelling is becoming increasingly recognized as an important research tool when studying collective behaviour. This is because it is usually not possible to predict how the interactions among a large number of components within a system result in population-level properties. By integrating behavioural rules into a simulation model and observing the resulting behaviour of the group, one has the opportunity to examine the sufficiency and necessity of these rules. If the predictions of the model fail to agree with the observations of the group's actual performance, then at least one important aspect of the behaviour is poorly understood and additional empirical investigations are needed to improve knowledge of how the group works. Once it is validated, the model can then be used to collect data that would not be available for experimental analysis, such as examining the relative importance of different features of the system and the effect of varying the magnitude of different parameters, and can thereby further increase our understanding of the biology of the study system. By combining mathematical modelling with experimental manipulations of group behaviour, it may become possible to understand important aspects of communication in insect larval societies, such as which individuals lead and why, which mechanisms are necessary for the cohesion of the group, and how groups "reach a consensus". A better understanding of the foraging mechanisms in social larval societies may in time provide insight into the evolutionary pathways of sociality.

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